3

Sexual Discrimination and Sound Production in *Uca pugilator* Bosc

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(Plate I; Text-figures 1 & 2)

Introduction

THE purpose of this study was to investigate sexual discrimination and to describe certain display behavior, including sound production, by males of *Uca pugilator*. Specimens and models with various combinations of male and female appendages were introduced to resident males. Sound production was observed and the sounds produced were physically analyzed.

The reproductive behavior of fiddler crabs (*Uca* sp.) has been investigated by many workers during the last fifty years. In all species, copulation is usually preceded by display behavior, consisting of the "waving" of the male's large cheliped. In some species, sounds are produced which play a role in courtship. "Waving" behavior is believed to define the territory of the male and attract females (Crane, 1941).

Sound production in *Uca* involves movements of the large cheliped. Dembowski (1925) described a peculiar "shivering" of the large cheliped in *U. pugilator*, lasting from one to three seconds, which was used by one crab to "call" another out of its burrow. Crane (1941) reported sound production by "rapping" of the cheliped against the ground in three Pacific American species of *Uca*, and in *U. pugilator* (Crane, 1943). Burkenroad (1947) made observations on *U. pugilator*. He did not believe that rapping of the cheliped was involved in sound production in this species, as he failed to detect any disturbance of sand grains below the cheliped of a male that had just produced sounds. No rattling of the dactyl or vibration of the body could be detected. He concluded that some other mechanism of sound production was utilized. Rathbun (1914) described ridges, thought to be stridulatory, on the large cheliped and ambulatory legs of male *U. musica*. Aurivillus (in Burkenroad, 1947) predicted, on morphological grounds, that stridulation would be found in the genus.

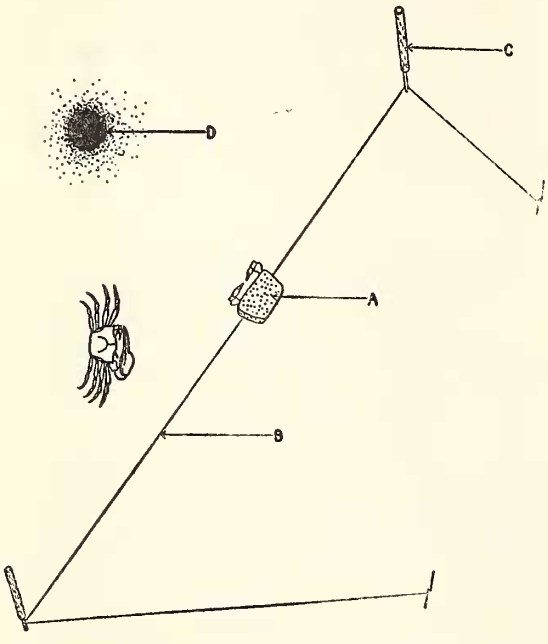
Burkenroad (1947) conducted experiments to investigate sexual discrimination in *Uca*. He released normal males, males without the large cheliped, and females of *U. pugilator* into an area occupied by resident males. In all cases, normal males evoked aggressive responses, but males without the large cheliped and females were courted by resident males. Altevogt (1957), working with *U. marionis* and *U. annulipes*, concluded that sexual discrimination by males was based on the presence of the large cheliped.

Materials and Methods

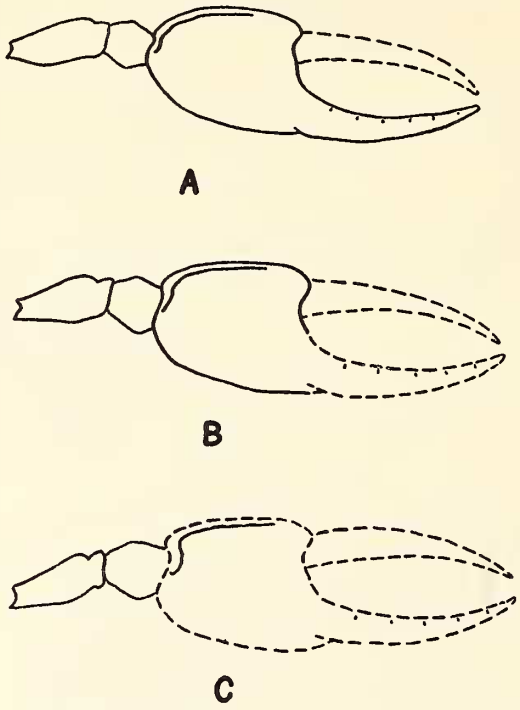
All observations and experiments were carried out on the west side of Pivers Island, Beaufort, North Carolina, during August, 1959 and 1961. The population of *U. pugilator* resided in clear areas of sand, either just above the high water mark or about 10 metres inland.

Sexual discrimination by males was investigated. In 1959, experiments were performed which repeated those of Burkenroad (1947). Males without the large cheliped, normal males, and females were released, in that sequence, and allowed to move through a 3 × 3 metre study area where over 40 males were exhibiting waving behavior. This sequence of releases was repeated ten times and the reactions of the resident males to all released specimens were recorded. In 1961, other introduction experiments were performed. A male that had previously exhibited waving behavior was frightened into its burrow. Two probes were placed in the sand about 0.6 metre to either side of the burrow

(Text-fig. 1). A dead specimen, killed by immersion in dilute alcohol, was placed between the probes. A long piece of thread was tied to a leg on either side of the body and then placed around one of the probes on the corresponding side and back about 1.5 metre toward the observer. The probes were placed in the sand so that by pulling the thread attached to either side of the dead crab, the specimen could be moved toward one or the other probe and within 7.5 cm. of the burrow. Dead specimens were introduced once to each of five resident males in this order: normal females; females with an attached large cheliped; normal males; and males with the large cheliped removed. Also introduced were two blue clay models of crab bodies. One model had two small chelipeds attached and the other, one large and one small cheliped attached to the anterior face. Each introduction consisted of slowly moving the dead crab or model from one probe to the other. After an experiment was completed, the male was frightened into his burrow. Another dead crab or model was prepared for the next test which was performed about five minutes after the male emerged from its burrow. Other introduction experiments were performed using live male



Text-fig. 1. A clay model (A) with two small chelipeds attached is used to demonstrate the technique employed in introduction experiments. By pulling the thread (B) from either side, the model could be moved between the probes (C) and through the resident male's territory. The male's burrow (D) was about 7.5 cm. from the model when it passed through the male's territory..



Text-fig. 2. The appearance of the large cheliped of live male *U. pugilator* used in introduction experiments to conspecific resident males. In the first trial, the dactylopod was removed (A); in the second trial, the anterior half of the protopod (B); and in the third trial, the protopod was completely removed (C). The parts of the claw outlined with dashed lines represent the removed portions of the appendage.

specimens. These were also tied with thread and moved between the probes as described above. Before each introduction, portions of the large cheliped were removed (Text-fig. 2, A-C). For the first introduction, the dactylopod was removed; for the second, the anterior half of the protopod; and for the third, the entire protopod. All three introductions were performed once in the order described until each of five additional resident males had been tested.

Sounds produced by males of *U. pugilator* were recorded with a Magnecorder tape recorder (model PT63-A) and a Dukane microphone (model 7A150). The microphone was suspended above or placed on the sand 2.5 cm. from the burrow. The sounds were analyzed with a Kay Electric Company Sonograph Model Recorder (B).

Results of Field Observations

Resident males and females defended an area of 7.5 to 15 cm. in diameter around their bur-

rows from intruders of the same sex. Four resident females each approached by another female advanced with chelipeds extended and open. The intruder female then retreated from the area. More than five resident males approached by intruding males exhibited aggressive responses as follows. The resident male oriented so that the large cheliped was held slightly away from the body and with its broad surface facing the intruder. If the intruder came within 7.5 to 10 cm. of the resident male, the latter advanced, opening its cheliped, until the broad surfaces of both individuals' large chelipeds came into contact. The resident then pushed the intruder from its burrow, using its cheliped as a shield. Occasionally, the resident male pointed its opened claw toward the intruder. If the intruder advanced, the claws of both individuals would be locked together and the intruder was either pushed or flipped away by the resident. If the intruder was more aggressive, the resident male retreated into his burrow but with the large cheliped opened and facing upward out of the entrance. Intruding females either evoked aggressive or courtship behavior from resident males, the latter occurring more frequently. Observations by the authors confirm those made by Crane (1943) on the features of waving exhibited by males. The chelipeds were raised upward and, at the same time, the animal rose on its "toes." The claws were then extended laterally and lowered, as was the body. Finally, the chelipeds were returned to the anterior margin of the body. The frequency of the waving motion was about once every two seconds when no female was present. When a female approached, the frequency increased to more than twice that rate. The claw was not brought back to the body, but raised and lowered while laterally extended. The male oriented so that the broad face of the claw was turned to the female. If the female moved toward him, the male would go toward his burrow in short spurts of 2.5 to 5 cm., starting as the claw and body were raised and stopping as they were lowered. In five observations, the female followed about 5 cm. behind the male as he moved toward his burrow. The male then entered the burrow, but the large cheliped remained extended out of the entrance. Waving of the large claw continued, but when lowered it was vibrated against the sand at the lip of the hole, producing a rapid series of thumps. Similar sounds were heard after the female entered the male's burrow. On four occasions, lone males were observed making these sounds in their burrows at night by hitting the base of the large claw against the side of the burrow.

Over fifty sounds produced by one male in his burrow were recorded during the day. A sonographic analysis of three sounds is presented (Plate I). Each burst of sound had a duration of 0.2 to 0.3 seconds. Of the 17 bursts analyzed, 7 consisted of 5 pulses; 5 of 4 pulses; 3 of 3 pulses; and 2 of 6 pulses. Each pulse was produced when the claw hit the surface of the ground as it was vibrated. The sound energy was concentrated between 85 and 2,000 cycles. With sounds of higher intensities, a suggestion of harmonics was present with frequencies up to 10,000 cycles.

Results of Introduction Experiments

The results of introduction experiments performed in 1959 were in agreement with those of Burkenroad (1947). Females and males without the large cheliped were courted, but normal males elicited aggressive responses from all resident males. Results of introduction experiments performed in 1961 are shown in Table 1. In all instances where dead crabs of either sex bore an intact large cheliped, the resident males responded aggressively. These responses were the same as those observed under natural conditions. When the dead introduced specimens bore no large cheliped, the resident males exhibited waving behavior and sound production typical of courtship. Neither waving nor aggressive responses were exhibited toward clay models with two small chelipeds attached. In two of five introductions, aggressive responses were exhibited to clay bodies bearing a large cheliped. Live male specimens with the dactylopod removed, and with the dactylopod and anterior half of the protopod removed, all evoked aggressive responses from resident males. Live males with the protopod removed were courted by four of five resident males.

Discussion

Even though the specimens and models were not introduced to resident males in a random order, the following tentative conclusions can be made. Sexual discrimination in *U. pugilator* is based on the presence or absence of the large cheliped, regardless of the sex of the specimen bearing the appendage. This appendage releases aggressive behavior in male-male encounters, and may be important in inducing sexual receptivity in females. The posterior portion of the protopod, the broadest surface of the claw, is capable of eliciting aggressive responses from other males, so that an intact claw is not necessary for sexual discrimination.

The large cheliped also functions as a sound-producing organ and the sounds have come to

play an important role in courtship. Burkenroad (1947) suggested that sounds substituted for the attractive qualities of the large cheliped when that appendage could no longer be seen by the female. He found that sounds were produced more frequently at night than during the day. The results of our field observations seem to support this view. When a male produces sounds during the day, he is partially hidden from the female by the lip of the burrow so that waving motions of the claw could no longer be effective visual stimuli. The waving motion is then modified to include a rapid vibration of the claw against the ground. The sounds produced either substitute for the visual stimuli of waving or may have other functions in courtship.

The results of sonographic analysis as well as field observations support the conclusion that stridulation is not used to produce sounds occurring during courtship in this species. A stridulatory sound is usually characterized by the concentration of the maximum energy in the higher frequencies. But rapid vibrations of the cheliped against the ground would be expected to produce thumping sounds which would show predominantly low frequency components such as those analyzed in this study.

TABLE 1. RESPONSES OF MALE *Uca pugilator* TO CONSPECIFIC MALES AND FEMALES AND TO CLAY MODELS[1]

Stimulus	Number of Responses		
	Waving	Aggressive Response	No Apparent Response
Dead Female	5	0	
Dead Female: large cheliped attached	0	5	
Dead Male	0	5	
Dead Male: large cheliped removed	5	0	
Clay Model: Two small chelipeds			5
Clay Model: one large, one small cheliped		2	3
Live Male: dactylopod removed	0	5	
Live Male: dactylopod and anterior half protopod removed	0	5	
Live Male: entire protopod removed	4	1	

[1] All tests with models and dead specimens were performed on the same five resident males. Live individuals were introduced to five other resident males.

SUMMARY

Courtship behavior of *Uca pugilator* was observed in a natural population. Waving behavior by males was exhibited when no female was present, but when a female approached a male, the waving motion was modified to produce sounds by vibrating the claw against the ground. A sonographic analysis of these sounds from one specimen showed that the energy of the sound was concentrated between 85 and 2,000 cycles and had a duration of 0.2 to 0.3 seconds. The role of sound production in the reproductive behavior of the species is discussed.

Sexual discrimination by males was studied by introducing models and specimens of either sex, bearing or not bearing the large cheliped (typical of male individuals), to resident males. In all cases, resident males exhibited aggressive responses to the specimens bearing the large cheliped and courted specimens without the large cheliped, regardless of the sex of the introduced specimen. It was concluded that the dominant visual cue in sexual discrimination was the presence or absence of the large cheliped.

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EXPLANATION OF THE PLATE

Plate I

Fig. 1. Sonographic analysis of three sounds produced by one male *Uca pugilator* in its burrow during the day.